

REFLECTIONS ON BEHAVIOR ANALYSIS AND EVOLUTIONARY BIOLOGY: A SELECTIVE
REVIEW OF EVOLUTION SINCE DARWIN—THE FIRST 150 YEARS.
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This review focuses on parallels between the selectionist sciences of evolutionary biology and behavior analysis. In selectionism, complex phenomena are interpreted as the cumulative products of relatively simple processes acting over time—natural selection in evolutionary biology and reinforcement in behavior analysis. Because evolutionary biology is the more mature science, an examination of the factors that led to the triumph of natural selection provides clues whereby reinforcement may achieve a similar fate in the science of behavior.

Key words: selectionism, evolution, natural selection, reinforcement, superstition, molar-molecular issue, genetics

Evolution through natural selection is arguably the major scientific achievement of the 19th century. But why should behavior analysis pay particular attention to developments in evolutionary biology during the 150 years since publication of Darwin's *On the Origin of Species*? The answer is that behavior analysis—uniquely among the behavioral sciences—also pursues a selectionist approach to complexity (Donahoe, 1983; 2003; Palmer & Donahoe, 1992). In a selectionist approach, complex phenomena are seen as the cumulative product of relatively simple processes acting over time. For Darwin, the relatively simple process was natural selection whereby differential reproductive success permitted the accumulation of heritable differences. The accumulation of these differences allowed them to become disproportionately represented in subsequent generations of a group of interbreeding organisms. For behavior analysis, the relatively simple process is reinforcement that differentially favors those behaviors that are followed by certain events called reinforcers. As a result, the products of selection by reinforcement become increasingly represented in the behavioral repertoire of a single organism. The present review explores the theme that the history of the more mature selectionist science of evolutionary biology

provides clues for behavior analysis in its efforts to understand complex behavior.

After a brief description of the general characteristics of selection processes, this review has two major sections. The first section examines the parallels between natural selection and selection by reinforcement. The second section identifies a somewhat surprising aspect of *Evolution Since Darwin* (ESD) and considers its implications for the future of behavior analysis.

Because of the focus of the present review, a number of important topics in this 39-author, 22-chapter monograph are not given the attention they merit. I mention only two here. The first deals with the history of evolutionary biology (see Kokkop & Jennions, p. 293). (The convention used here for referring to work in ESD is to cite the name of the author followed by the page number as appropriate.) Bowler's chapter speculates about what the current state of evolutionary biology would be if the genetic mechanisms of heredity had been discovered *before* the principle of natural selection. (Bowler's book *The Eclipse of Darwin*, 1983, recounts the years between publication of *The Origin of Species* and the acceptance of natural selection within biology, and is known to readers of JEAB; Catania, 1987). Bowler provocatively concludes that "...a world without Darwin is ... something that would look remarkably like the extreme (i.e., nonselectionist) version of modern evolutionary developmental biology" (p. 43). That is, instead of the functional stance to complexity encouraged by natural selection, evolutionary biology

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would have acquired a structuralist cast focusing primarily on the mechanistic details of development and morphology. A second topic that is omitted from the present review is human evolution. White's chapter provides an overview of paleontological research on human origins that belies the sometime claim that the fossil record of human evolution is uncharacteristically sparse. In fact, the study of human origins is an extremely active and productive line of current work both at the paleontological level (e.g., Carlson et al., 2011) and the molecular level (e.g., Edinborval et al., 2011; Noonan et al., 2006; Yotova et al., 2011). For example, much has been made of the finding that humans and chimpanzees share approximately 98% of their structural genes (that is, protein-coding genes) in common. However, the regulatory genes that govern the action of structural genes differ greatly from chimpanzees and are much less variable in humans than other species (King & Wilson, 1975; Kirkpatrick, p.181ff). Further, the sheer number of genes is not correlated with complexity: The human genome contains about 20,000 genes whereas the rice genome contains over 40,000 genes. Our species appears to be the product of the natural selection of a very restricted combination of a relatively small number of genes (Wray, p. 234). Although the genetic composition of humans and other species is increasingly known, a recurring theme in *ESD* is that the relation between the genome and phenotype remains an unsolved puzzle. As several contributors put it, "...the molecular genetic basis of organismal complexity remains largely unexplained" (Zhang p. 97), "inferring phenotypic effects from nucleotide changes remains challenging" (Schuler, p. 283), and "compared to our knowledge of genomes, our knowledge of phenotypes remains cursory" (Hoekstra, p. 642). Finally, I would note that *ESD* is uniformly well written and assiduously edited.

THE NATURE OF SELECTION PROCESSES

Darwinism, or *selectionism* as the approach is more generally known, provides an account of the origins of complexity that does not entail principles that directly impose complexity (Richerson & R. Boyd, p. 361). Instead, complexity is a possible—although not inevitable—outcome of the repeated action of lower-order

processes. As a general approach, the potential range of selectionism extends far beyond evolutionary biology. Any limitations of selectionism arise primarily from pretheoretical commitments—particularly the sort of implicit rationalism that pervades many accounts of human behavior, as in much of linguistics and cognitive psychology (Donahoe, 1983). Selectionism has been productively instantiated in such diverse fields as the design of electronic circuits (Holland, 1975; 1992), economics (Harford, 2011), and cosmology (Smolin, 1997).

A selection process consists of three interdependent phases—variation, selection, and retention. *Variation* provides the raw material upon which selection operates. It is the source of whatever novelty arises from repeated cycles of the selection process. Selection acts only on already existing variants. This is clearly recognized in evolutionary biology where Wakely comments in *ESD* that "natural selection can occur only if individuals of a species vary" (p. 119). Using Donald Campbell's term, variation is "undirected" (Campbell, 1974). That is, variation occurs independently of the selecting factor. The second phase of a selection process is selection itself. *Selection* leads, potentially, to complexity when some event acting on the population of variants favors (or disfavors) one variant over another. Selection confers to the process the illusion of purpose when the selecting contingencies remain constant or change slowly over time. Selection processes are not directed in a teleological sense. The future does not pull the present toward itself; instead, the past pushes the present into the future. The trajectory of selection depends utterly on the relative constancy of the selecting contingencies and the population of variants. Future contingencies are "anticipated" only insofar as they have been encountered in the past. *Retention* is the third phase of a selection process. Retention permits selected variants to persist long enough for them to contribute to the variation upon which future selections act. Without retention, selections cannot accumulate and even the possibility of complexity is precluded. (For discussions of the implications of selectionism for behavior, see Catania, 1995; Donahoe & Wessells, 1980; Donahoe & Palmer, 1994; Palmer & Donahoe, 1992; Skinner, 1953; 1966; and Staddon & Ettinger, 1989. For more general philosophical treatments, see Dennett,

1995; Gayon, 1992; Hull, 1973; Mayr, 1988; and Sober, 1984.)

PARALLELS BETWEEN NATURAL SELECTION AND SELECTION BY REINFORCEMENT

ESD recognizes the importance of environment-behavior relations in natural selection. For example, "This flood of genetic data will be of little use to evolutionary biologists unless the ecological context of the organism's place in the environment is well understood (McPeck, p. 345). Or again, "a change in animals' morphology is often preceded by that in behavior" and "the connections among genes, neural circuitry, and the evolution of complex and adaptive behavior remain a major frontier in biology" (Hoekstra, pp. 645-646). Darwin himself is approvingly cited to similar effect: "A shift into a new niche or adaptive zone is, almost without exception, initiated by a change in behavior" (cited in Mayr, 1963, p. 604). However, despite these acknowledgements, essentially nothing about the scientific study of behavior appears in *ESD*. Watson and behaviorism are briefly mentioned as ensuring that "behavioral studies became increasingly quantitative and less anthropomorphic" and as providing "the first tools to identify and quantify behavioral traits" (Kokko & Jennions, p. 293). But neither Watson nor behaviorism appear in the extensive index and Skinner and other behaviorists are ignored altogether, even though a substantial literature exists on the parallels between selection by reinforcement and natural selection. In fact, some contributors to *ESD* mistakenly—if understandably—echo the widely circulated, but mistaken view (e.g., Simon, 1980), about "the limitations of [the behavioral approach] when dealing with species for which a theory of mind seems essential" (Kokko & Jennions, p. 293). Reading this comment, students of Skinner may take some comfort from the following statement about Darwin's views: "Subsequent scholarship on human evolution frequently attributes ideas to Darwin that cannot actually be found in his writings, but only in secondary, tertiary, or even more derived and less accurate sources" (White, p. 522).

Variation

Before examining the parallels between the three phases of a selection process in natural

selection and in selection by reinforcement, it should be obvious that the parallels are functional, not structural. That is, the physical events and mechanisms implementing the three phases differ, but the effects of the phases are conceptually related. In the case of natural selection, variation refers to differences between the characteristics (the phenotype) of *different* organisms within a breeding population. The population of variants in the selection of behavior is fundamentally different. Here, variation refers to differences within the population of behavior (the behavioral repertoire) of a *single* organism. The distinction between the populations upon which selection operates is what motivates the methodological divergence between the study of the behavior of *individual* organisms in behavior analysis and of *groups* of organisms in normative psychology. Normative psychology uses group methodologies that were devised for the study of natural selection, not the individual methodologies that are appropriate for selection by reinforcement (cf. Sidman, 1960). On those occasions when behavior analysts use group methodologies, it is typically to report their findings in a manner that communicates more effectively with other behavioral disciplines.

Variation in evolutionary biology. The discovery of the genetic basis of inheritance more than 40 years after *On the Origin of Species* led to the ability to identify differences between individuals at an observational level below the phenotype, namely the genotype. As the philosopher of biology Gayon recognized, "It was through its contact with the new science of heredity that the theory of selection became truly intelligible" (Gayon, 1992, p. 253). The integration of Darwinian selection with heredity is known as the modern synthesis in biology (Huxley, 1942). The physical basis of genetic variation includes mutation (changes in alleles caused by exogenous agents such as chemicals and radiation), recombination (intermixing of alleles during reproduction), genetic drift (random sampling of alleles, especially at the molecular level), and gene flow (migration of genes between populations). Of course, Darwin knew nothing of the genetic basis of inheritance and was unaware of Mendel's work, although one unopened book with a citation to Mendel has been found in his library (Zhang, p. 88). Even after knowledge of

Mendel's work on the particulate inheritance of phenotypic traits became widespread, the gene remained only an inference from observation (a hypothetical construct). For that reason, the gene was at first not accepted into mainstream biology by none other than Thomas Hunt Morgan, later considered "the father of the gene."

In the modern interpretation of Mendelism, facts are being transformed into factors [i.e., genes] at a rapid rate. If one factor will not explain the facts, then two are invoked; if two prove insufficient, three will sometimes work out. The superior jugglery sometimes necessary to account for the results may blind us . . . to the commonplace that the results are so excellently 'explained' because the explanation was invented to explain them. We work backwards from the facts to the factors, and then, presto! Explain the facts by the very factors that we invented to account for them. (Morgan, 1909; cited in Shine & Wrobel, 1976, p. 51)

Behavior analysts will recognize in Morgan's early reservations about the gene Skinner's kindred reservations about the fantasy physiology of his day (Skinner 1938; 1950). It was only after Morgan's experimental work permitted direct observation of the giant chromosomes of the salivary gland of the fruit fly that he welcomed the gene into the science of heredity.

Variation in behavior analysis. From the very beginning, variation was regarded as fundamental by Skinner (1935). Little was known about its biological basis but Skinner conceived of both the environment and behavior as *classes* of events. The conjunction of instances of environmental and behavioral events with a reinforcer selected variants within those classes. The membership of the classes changed from moment to moment. Thus, in successive moments a light that functioned as a discriminative stimulus in an operant chamber might be seen by the rat from different angles at somewhat different intensities and a lever press that was followed by a reinforcer might occur with different forces and topographies. Skinner was not alone in acknowledging the inevitability of variation in the controlling stimuli. Skinner's former student William Estes later developed a mathematical theory that explicitly implemented variation in the stimulus, to wit, stimulus-sampling theory (Estes,

1950). (See Guthrie, 1935, for a molecular view of the nature of the response in his distinction between movements and acts.) Later work at the neural level amply documents variation within both stimulus and response classes. That is, a stimulus of constant physical characteristics activates a variable subset of receptors as their thresholds and habituation rates change. Similarly, the same behavioral response is the concerted product of the activity of varying members of a population of motor neurons and of the muscle fibers they innervate (Georgopoulos, Schwartz, & Ketner, 1986). Finally, the neurons in the brain and spinal cord that intervene between sensory and motor neurons are a variable subset of the cells in the central nervous system. Thus, at the neural level, successive instances of the "same" stimulus and response are never identical.

The variation between behavioral responses within a given environment (the behavioral phenotype) is the variation upon which reinforcers are contingent. It is this variation from which reinforcers select, and only indirectly the neuromuscular events with which the environmental and behavioral events are correlated. As the evolutionary and conditioning histories of the organism become more extensive, the various stimuli that may be sensed in that environment come to control different responses at differing strengths. The strengths of these responses depend on which stimuli are sensed at the moment and the details of their history with respect to those stimuli. Some environment-behavior relations are relatively constant over evolutionary time and become reflexive relations through natural selection. Reflexes can be relatively simple, such as the pupillary response to changes in illumination, or can be quite complex, such as the whole-body righting reflex in response to gravitational cues. However, the major source of variation for the emergence of complex behavior is to be found in the history of reinforcement. For example, if different responses have been conditioned to different elements of the same environment, which response occurs at a given moment depends on such variables as the prior frequency of reinforcement for those responses. Depending on the details of that history, one response may be dominant at one moment and a different response at another, even in the same generic

environment (e.g., Blough, 1966; Notterman, 1959; Palmer, in press). An organism's history of reinforcement is an increasingly important contributor to behavioral variation just as a species' history of natural selection is an increasingly important contributor to morphological variation.

Selection

Selection is the second phase of a selection process. In the case of evolutionary biology, natural selection acts on the phenotypic variants and, less directly, the genetic variants with which they are correlated. Natural selection changes the relative frequencies of genes in a population of different organisms in a subsequent generation. In the case of behavior, selection by reinforcement changes the relative frequencies of behavior (and indirectly the physiological events with which they are correlated) in the behavioral repertoire of the same organism on subsequent occasions. The following discussion focuses on how selection operates in the two cases.

Natural selection. The selecting agents in natural selection arise from the environments in which the variants occur. This includes not only the external environment—both its physical and organic elements—but also the intra-organismic environment of the organism in so far as these environments affect reproductive fitness. Because of variation in the conjunctions of phenotypic traits that coexist in a given organism as well as the vagaries of the selecting environment, the outcome of selection is probabilistic. For example, George Washington undoubtedly possessed many qualities that usually favor reproductive success, but he left no children although his wife was known to have been fertile given that she had children from a previous marriage. The outcome of natural selection is further complicated by the fact that it is not the traits that survive (i.e., are retained) and passed to the next generation but the genes only. Moreover, most traits—particularly behavioral traits—are influenced by multiple genes. Speaking metaphorically, traits are the shadows on the walls of Plato's cave and genes are the objects that cast the shadows. The selecting environment "sees" only the shadows, but the same objects may sometimes cast different shadows. The phenomenon of genetic hitchhiking nicely illustrates these complications (Wakely, p. 127).

Suppose that a favored phenotype is correlated with a gene at a particular locus on a chromosome and that another gene located at a nearby position on the same chromosome is not so correlated. Because the two genes are adjacent, natural selection is likely to increase the frequency of both genes in subsequent generations because recombination is less likely to separate them. "Selection for" the advantageous gene results in "selection of" the hitchhiking gene, to use Sober's (1984) terminology. Genetic studies in humans indicate that hitchhiking affects perhaps 10% of the genes in the genome.

Darwinism has confronted several serious challenges during the past 150 years. One is altruism in which an organism acts to reduce its individual reproductive fitness but, in so doing, enhances the fitness of others. The initial reaction of some evolutionary biologists to this phenomenon was to promote a molar conception of natural selection. If the fitness of the *group* to which the sacrificing individual belonged was increased, then perhaps overall fitness might be enhanced (Wynne-Edwards, 1962). However, Hamilton (1964) showed that these phenomena did not require a shift to a more molar, group-level view of selection. Instead, altruism could be understood by recognizing that what was retained were the genes *per se* and that the individual in which they reside is irrelevant. If the sacrificer and the beneficiary share genes in common, then altruistic behavior presents no fundamental challenge to natural selection. Summarizing his brief review of altruism, Futuyma (p. 18) concluded that the groups in molar models "are almost always kin groups [i.e., genetically related], so that kin selection and group selection are two ways of describing the same process."

A second challenge to Darwinian selection came from those who questioned whether the evolutionary process was gradual, as Darwin had proposed, or proceeded in discrete steps that were constrained by species-specific characteristics. Proponents of the gradualist position referred to the saltationist position (i.e., punctuated equilibrium) as "evolution by jerks" (Turner, 1984) whereupon the saltationists responded in kind by referring to the gradualists as "evolution by creeps" (Gould & Rose, 2007, p. 6). (Such is the dispassionate nature of science!). In his summary of the outcome of this debate, Futuyma concluded that with respect to the claims of species-level

selection by the saltationists, the "challenge to the synthetic theory failed" (p. 19).

A final major challenge to the Darwinian account of biological evolution came from those who argued for the importance to evolution of random genetic changes at the molecular level, so-called neutral-gene theory (Kimura, 1968). There was general agreement that random genetic changes contributed to variation, but sharp disagreement about how or whether it affected the course of evolution. The historian of science William Provine took delight in this controversy: "It's the greatest topic in the world. I can't even begin to tell you how much fun it is. People just fight like crazy" (cited in Blum, 1992). Of this debate, Wakeley (p. 143) concluded that a neutral-gene theory of evolution should be abandoned "given the lack of force of theoretical arguments for the neutral theory, the empirical evidence against it, and the fact that the selective models can ... provide a better fit to the observations and mimic neutrality itself." As a case in point, one analysis estimated that "about 50% of [molecular] substitutions will be driven by positive selection in *Drosophila*" (Wakeley, p. 128).

The general conclusion from these three challenges to the role of natural selection in evolution is that the selectionist account has prevailed, whether challenged from a more molar or more molecular perspective. Be that as it may, confronting these challenges strengthened the Darwinian view by showing that it could be extended to accommodate an ever wider range of phenomena at many levels of observation (but see Crow, 2008).

Selection by reinforcement. How does selection occur in selection by reinforcement? Skinner's view was that "the environment selects behavior" (Skinner, 1985, p. 291) but he was silent on the nature of the selecting event. He believed that neuroscience would eventually identify the physical basis of selection by reinforcement, but that much behavior could be understood without characterizing the reinforcing event. Reinforcers were simply stimuli that, on subsequent occasions, increased the relative frequency of those responses with which they were contingent. (See Meehl, 1950, for a critique of this view.) Skinner's position had ample precedent. Darwin showed that important insights into evolution could be achieved by adopting a selectionist stance

even when the mechanisms of selection were unknown. Skinner held that nothing that was eventually learned about the physiology of behavior could undermine valid behavioral laws (Skinner, 1938, p. 432). The only requisite for selection by reinforcement that Skinner (and many others) identified was that the reinforcer must occur immediately after the behavior to be selected. "To say that a reinforcer is contingent upon a response may mean nothing more than that it follows the response ... conditioning takes place because of the temporal relation only, expressed in terms of the order and proximity of response and reinforcement (Skinner, 1948, p. 168). This is generally known as the temporal-contiguity requirement.

In the late 1960s, it became clear that something in addition to contiguity of a putative reinforcer with behavior was needed (Kamin, 1968; 1969). It was found that if a response had been conditioned to an antecedent stimulus and that same response was later followed by the same reinforcer in the same environment but preceded by a newly introduced antecedent stimulus, then the new stimulus would not acquire control of the response (Rescorla & Wagner, 1972; Vom Saal & Jenkins, 1970). What else was needed? Subsequent research indicated that a stimulus functions as a reinforcer if it not only occurred in temporal contiguity with a response but also evoked activity that was not otherwise occurring in that environment (Donahoe, Burgos, & Palmer, 1993; Donahoe, Crowley, Millard, & Stickney, 1982). This holds true whether the change in activity occasioned by the reinforcing stimulus was the result of prior natural selection (Stickney & Donahoe, 1983) or prior selection by reinforcement (Palmer, 1987), and whether the activity was observable at the behavioral level of observation or only at the neural level (e.g., Tobler, Fiorillo & Schultz, 2005). On this view, a stimulus functions as a reinforcer only when it evokes a *change* in activity. For example, if bar pressing by a rat is followed by "unexpected" food, then both bar pressing and salivating are increased in that environment. Natural selection has produced a learning mechanism by which the organism is adapted to the *new* behavioral demands of its environment. And, to the extent that the learning mechanism enables adaptation, the organism is buffered from the effects of

natural selection for those environment-behavior relations (cf. Richards, 1987). It is in this sense that “learning is the pacemaker of evolution” (Wilson, 1975, p. 156). As with natural selection, selection by reinforcement “prepares” the learner to behave in the future as it has in the past with regard to the selecting contingencies.

Also, as with natural selection, “selection for” a particular response may result in “selection of” another response with which it is correlated. This is the phenomenon of superstitious conditioning (Skinner, 1948) and is the counterpart of genetic hitchhiking in natural selection. Superstitious conditioning is further testimony to the generic nature of the stimuli and responses on which selection by reinforcement acts. I recall a situation in which a colleague trained in associative learning asked his research assistant to condition lever-pressing with a number of rats in operant chambers in my laboratory, but not to use shaping. In this way, the “natural process of learning” could occur. After some time, the research assistant complained that one of the rats was pressing much more slowly than the others and, moreover, that loud “thumps” were occasionally coming from the chamber. When I looked into the chamber through the magnifying peephole, I discovered that the rat was hurling itself against the transparent ceiling of the chamber and extending its leg to catch itself as it fell. In so doing, the rat pressed the lever. Apparently, the previously feeder-trained rat had tried to leap out of the chamber and had inadvertently pressed the lever in the process.

The foregoing view of selection by reinforcement is based on momentary contingencies of environmental and behavioral events with reinforcers, and is in keeping with Skinner’s (1948) account in that respect. However, as with group-selection challenges to Darwinian selection based on *groups* of individuals, conceptually similar challenges have arisen to momentary accounts of selection by reinforcement based on groups of responses. For example, orderly relations have been found between the number of reinforcers and the number of responses during exposure to concurrent schedules, the so-called matching relation (Baum, 1973; 2002). Research has uncovered momentary relations between stimuli, responses and reinforcers that can produce molar relations (e.g., Burgos & Murillo-Rodriguez, 2007; Crowley

& Donahoe, 2004; Hinson & Staddon, 1983; McDowell, 2004). However, the most effective level at which to formulate selection by reinforcement remains controversial (Baum & Davison, 2009).

Retention

The third phase of a selection process is retention. Retention permits the selected variants to endure long enough for them to contribute to the pool of variation upon which future selections act.

Retention in evolutionary biology. As already noted, what are retained in natural selection are the genes, not the traits, which are the complicated expression of the genes’ interactions with the environment of the individual. Darwin’s prescient accounts of many evolutionary phenomena testify to the power of selectionist thinking even when the mechanisms that implement it are unknown. The story of Darwin’s transition from his theory of “gemmules”—whereby hypothetical entities migrated from somatic cells to influence germ cells, to his version of the inheritance of acquired characteristics—whereby he attempted to counter the mathematical arguments of Fleeming Jenkin (Gayon, p. 85 ff), will not be reviewed here. The rediscovery of Mendel’s work—after an initial over-emphasis on the role of mutation by DeVries—led to the modern science of genetics in which genes are passed unchanged, save for mutation, from parent to offspring. Genetics and molecular biology have revealed the objects whose shadows are cast on the walls of Plato’s cave.

There is one exception to the immutability (immortality?) of genes that merits attention here—epigenetics (Futuyma, p. 21; Wray, p. 235; Richerson & Boyd, p. 582). Epigenetics is concerned with the effects of the parental environment on the genes that are passed to their offspring. Epigenetic changes have been found to endure over several generations (Seong et al, 2011). As one example, rat pups which were stressed when raised by inattentive mothers were found to have methyl groups ($-CH_3$) bound to their genes. (The genes themselves were not otherwise affected). The methylated genes were later found in their offspring as well (Gräff, Franklin, & Mansuy, 2010). Similar epigenetic effects have been reported in humans. Stress methylates the maternal genes and the genes of their offspring

become methylated in turn. As a consequence, the response of the corticotropin receptors of the offspring are altered, which affects their reaction to stress (Oberlander et al., 2008). A possible evolutionary interpretation of these epigenetic effects is that, if a condition is present in the parental environment, then that same condition is also likely to occur in the environment of the offspring. Epigenetics is a currently active and somewhat controversial area of research whose implications for a variety of phenomena, including memory, are being studied (e.g., Miller, 2010).

Retention in selection by reinforcement. Retention of the effects of selection by reinforcement is dependent on the stimuli in the present environment and in the public and private behavior selected by reinforcers in the past in that environment. (See the discussion of reminding and remembering in Donahoe & Palmer, 1994/2010.) Just as a flood may reveal fossils previously covered by sediment on a river bank, so may extinction of a dominant response reveal behavior that was too weak to appear until stronger responses have weakened (Cançado & Lattal, 2011; Epstein, 1985; Palmer, in press; Shahan & Sweeney, 2011). The retention of behavior is mediated by the effects on the nervous system of prior selection by reinforcement. If tracing the path from genes to traits is a daunting task, then how much more so is the path from neurons to behavior! There are “only” about 20,000 structural genes (although many additional regulatory genes) in the human genome but there are perhaps 100 billion neurons in the human brain connected to one another by over 100 trillion synapses. The next and final section of the review describes how evolution through natural selection has confronted the challenge of tracing the trajectory of evolutionary change and outlines a similar strategy for behavior analysis in its effort to understand complex behavior as the product of selection by reinforcement.

SELECTIONIST APPROACH TO COMPLEX PHENOMENA

What was most welcome to a behavior analyst reading *ESD* was the unequivocal acceptance of selectionism—in the form of natural selection—as the origin of complexity. Oh that selection by reinforcement would occupy such

an exalted position! Consider some of the following statements from *ESD*: “All of molecular biology and genomics triumphantly affirm the unity of life and its common ancestry” (Futuyma, p. 7). “Natural selection is the primary force driving evolutionary change ... Despite the huge diversity of life at the organismal and genomic levels, there are universal rules of evolution ... [and] ... these rules may be discovered by studying a relatively small number of species” (Zhang, pp. 88, 93). Contrast the last statement with Simon’s (1980) criticism that behaviorism has a “preoccupation with laboratory rats rather than humans engaged in complex thinking and problem-solving tasks” (p. 76). And, most pointedly, contrast Simon’s views with the following comment of Darwin, “He who understands baboon would do more toward metaphysics than Locke” (Richerson & Boyd, p. 562, citing Darwin’s notebooks M and N in Gruber & Barrett, 1974, p. 281). Finally, “...a complete understanding of any issue in biology requires an explanation of its evolutionary origin...” (Zhang, p. 108). Because natural selection is universally accepted in evolutionary biology, *ESD* is not forced to defend it with experimental work but is freed to pursue its implications. In short, the bulk of *ESD* is devoted to scientific *interpretation*, not experimental analysis, to use Skinner’s terms for the distinction (Skinner, 1957).

How did natural selection come to occupy center stage in evolutionary biology while selectionism struggles in behavioral science? Our understanding of the details of selection by reinforcement is arguably at least as complete as was Darwin’s understanding of natural selection. The answer lies in two directions. First, knowledge of the biological mechanisms implementing natural selection—genetics and molecular biology—are much more advanced than our current understanding of the neural mechanisms of selection by reinforcement. Second, quantitative methods for exploring the implications of natural selection are much more developed than those for tracing the effects of selection by reinforcement. Let me briefly comment on each of these.

In the desire to establish an independent science of behavior, some have sought to separate behavior analysis from the other biological sciences because of fear that the independence of behavior analysis would somehow

be compromised (e.g., Reese, 1996; cf., Donahoe, 1996). Skinner regarded behavior analysis as "...a rigorous, extensive, and rapidly advancing branch of biology ..." (1974, p. 255) but, in spite of this, some contemporary theorists denigrate a concern with the biological basis of behavior: "Neurophysiology may be omitted ... because it reveals only mechanism" (Baum, 2011, p. 119). While it is true that an experimental analysis of the neural mechanisms of conditioning presents formidable challenges, a great deal of progress is being made on this front (e.g., Frey, 1997; Redondo, Okuno, Spooner, Frenguelli, & Morris, 2010; Sweatt, 2010). Be that as it may, it is nevertheless also true that the complexity of the nervous system and our irremediable ignorance of the complete history of selection by reinforcement forever preclude a full *experimental* analysis of any particular instance of complex behavior. These difficulties are not unique to behavior analysis, but are shared with all historical sciences (Donahoe, 1997a; Donahoe & Palmer, 1989)—including evolutionary biology. However, unlike evolutionary biology, behavior rarely leaves any fossils that are visible to the unaided eye (Tinbergen, 1963). The physical fossils of behavior are forever hidden among the myriad synapses of the nervous system.

How does evolutionary biology address its conceptually related difficulties? Evolutionary biology has developed quantitative procedures for tracing the effects of natural selection on a population of variants. Indeed, the development of statistical procedures for tracking gene flow played an essential role in the modern synthesis of genetics with natural selection (Fisher, 1930; Haldane, 1932; Wright, 1968). These mathematical techniques permitted gene flow between species and generations to be followed in a rigorous fashion and thereby demonstrated that the changes proposed by Darwin could, in fact, occur. "Today, evolutionary theory is properly framed in mathematical terms and with reference to the genetics of populations" (Gardner, 2010). The salutary role of quantitative procedures in evolutionary biology is acknowledged in many places within *ESD*, and not only with respect to genetics. "Paleontologists have taken advantage of advances in biological theory and quantitative methods to predictably and quantitatively summarize patterns that Darwin could

only describe verbally and to articulate predictions for Darwin's models that Darwin himself was unable to derive" (Wagner, p. 451). "Although Charles Darwin had amazing vision, he could not have imagined the technology that would allow biologists to reconstruct and utilize the Tree of Life..." (Hillis, p. 445). Among the quantitative methods developed in response to the complexity of evolutionary biology is simulation research, which is made possible by modern computer technology (e.g., Lewontin & White, 1960; Maynard-Smith, 1964). Computer simulations permit the implications of principles to be pursued when they are too complex for closed-form analytical solutions. Although simulations can only partially capture the salient features of the history of interactions of organisms with their environments, they provide a kind of "existence proof" that complex phenomena are within the competence of natural selection (Kokkop & Jennions, p. 293; Wagner, p. 455).

Behavior analysis has also recognized the need for dynamical quantitative procedures (e.g., Marr, 1992) and has begun to use them to interpret the outcome of selection by reinforcement. These quantitative procedures have been implemented at various levels of analysis. All such work is constrained by behavioral research but it may also be informed by findings at other levels of analysis. Some quantitative work in the interpretation of behavior is informed by neuroscience (e.g., Donahoe, 1997b), some by evolutionary considerations as well as neuroscience, as in hybrid genetic/learning algorithms (Burgos, 1997; Donahoe, 2002), some by evolutionary considerations using genetic algorithms (McDowell, 2004), and others by largely behavioral considerations alone (Hutchison, 1997; Killeen & Fetterman, 1988). Quantitative work need not reflect all of the potentially relevant science. However, to qualify as a *biobehavioral* interpretation—and not merely mathematical modeling—the methods must not be demonstrably inconsistent with such information. Purely conceptual constraints, for example, that the quantitative procedure must produce optimal solutions, should be regarded with caution although they may serve as useful reference points against which to compare quantitative results (Kokkop & Jennions, p. 299). An evolutionary biologist remarked that the belief that "selection generates optimal solutions

cannot be defended as an accurate view of the real world" (Gardner, 2010) and the same is equally true of behavioral selection as well. An organism is the focus of many selecting contingencies over its individual and evolutionary history and the chance that performance will be optimal in any one case is remote. Finally, there is no one "correct" level at which to trace the effects of selection by reinforcement. As Skinner (1935) recognized much earlier, the appropriate level is the one at which order emerges with respect to the phenomenon under study. This applies to quantitative as well as experimental procedures.

Lastly, because evolutionary biologists and behavior analysts share a common commitment to selectionism, fruitful collaborations should be sought to unravel the secrets of conditioning and memory, and how they are affected by genetics. The development of operant conditioning preparations for the zebrafish would seem especially promising because there is a substantial relevant research literature—on conditioning with fish (e.g., Hollis, 1997), on the genetics of zebrafish (Detrich, Westerfield, & Zon, 2004), on the relation of zebrafish genetics to behavior (e.g., Wolman & Granato, 2011), and on the NMDA receptor which is known to play a central role in vertebrate conditioning (Sison & Gerlai, 2011).

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